LXV.—*On the Change and Form of the Teeth in the* Centetidæ, *a Malagasy Family of Insectivora.* By C. I. Forsyth Major.

Among the fruits of my two years' sojourn in Madagascar is a rich series of recent Insectivora (Centetidæ), and since a considerable time must still elapse before this is completely worked out in a monograph *, I now give in a condensed shape in the following pages the most essential facts as to the change and form of the teeth in the family in question, so far as it has yet been possible to render the material available for examination.

A.

The Change of the Teeth.

Oryzoryctes tetradactylus.

Stage I. *I.d.* 1 and *I.d.* 3 have come through almost completely; of the remaining milk-teeth the tips alone protrude. The *C.d.* are the most backward.

Stage II. All milk-teeth protrude from the jaws to their full extent, with the exception of *C.d.*, of which the posterior basal cusp is not yet visible. *M.* 1 begins to protrude.

Stage III. Skull somewhat shorter than in II.—All milk-teeth are completely protruded, with the exception of *C.d. inf.*, of which the posterior basal cusp is not yet visible. The greater portion of *M.* 1 is protruded

Stage IV. All milk-teeth completely protruded, as also *M.* 1; *M.* 2 partly so.

Stage V. Like IV.; but *M.* 2 is further advanced. *I.d.* 3 *sup. dext.* on the point of falling out.

Stage VI. Skull somewhat longer than in VII. and VIII.—*M.* 1 is *in situ*; *M.* 3 *sup.* and *inf.* on the point of coming through. *I.d.* 1 and *I.d.* 3 *sup.* and *inf.* have been shed. *I.* 3 *sup.* and *inf.* altogether *in situ*; *I.* 1 *sup.* not yet completely so. *I.* 1 *inf.* is more backward on the right than on the left. *P.* 3 (Hens.) is commencing to raise *P.d.* 3.

Stage VII. Skull a shade longer than that of VIII.—*M.* 3 *sup.* is somewhat further advanced than in the latter, *M.* 3 *inf.* somewhat more backward. In the change of teeth VII. is somewhat less further advanced than VIII.

* The diagnoses of most of the new species have already been published. *Cf.* Ann. Mag. Nat. Hist. ser. 6, vol. xviii. 1896, pp. 318–322, 461–462.

Upper jaw: *I.d.* 3 has been shed and its successor is *in situ*; *I.d.* 1 has likewise disappeared, *I.* 1 not yet completely *in situ*; *I.d.* 2 still present on both sides. *P.d.* 3 still rests like a cap upon its successor. Lower jaw: *I.d.* 1 has been shed, but its successor has not yet come through completely. *I.d.* 3 has likewise been shed, and its successor is *in situ*; *I.d.* 2 is still present. *P.d.* 3 has been shed, *P.* 3 is not yet completely protruded. *C.d.*, *P.d.* 2, and *P.d.* 1 are still in place above and below. *M.* 3 *sup.* and *inf.* are nearly *in situ* and already partly in use.

Stage VIII. *M.* 3 almost protruded above, entirely so below. Upper jaw: The change of the anterior and posterior pairs of *I.* has been consummated, and the permanent teeth are *in situ*. *I.d.* 2 is still present on the left side; on the right it has been shed, and *I.* 2 is beginning to appear. In the lower jaw the change of the anterior and posterior pairs has likewise taken place, and *I.* 1 and *I.* 3 are *in situ*; *I.d.* 2 is still present on both sides, as are also all four *C.d.* *P.d.* 3 has disappeared above and below, and the *P.* 3 are almost completely in place. The posterior milk-premolars (*P.d.* 1 and *P.d.* 2) are still present.

Stage IX. But little further advanced than VIII.—*M.* 3 *sup.* is *in situ* as well as *M.* 3 *inf.* The only other difference from VIII. consists in the fact that *I.d.* 2 has been shed on both sides; *I.* 2 is not yet *in situ*. The tip of *C. sup.* is visible, *in front* of *C.d.*; *C. inf.* is coming into view on the inside of *C.d.*

Stage X. The change of the whole of the teeth is accomplished. *C.* is not yet completely *in situ*, and is consequently the last tooth to be replaced, as also its precursor is the last to appear in the milk-dentition.

Oryzoryctes hova.

Stage I. All milk-teeth *in situ*. *M.* 1 is almost entirely exposed; *M.* 2 is beginning to protrude.

Stage II. Milk-teeth as in I. *M.* 1 and *M.* 2 somewhat further advanced, *M.* 1 *inf.* completely *in situ*.

Stage III. *I.d.* 1 and *I.d.* 3 have been replaced above and below; *I.d.* 2 and likewise *C.d.* are still *in situ*. *P.d.* 3 *sup.* has been shed on the right, on the left it still rests like a cap upon *P.* 3, which is coming into position. *P.d.* 1 and *P.d.* 2 *sup.* and *inf.* are still *in situ*. All three molars are completely developed and *in situ*.

Microgale Dobsoni.

Stage I. All molars functional. In the upper jaw the whole of the milk-teeth are still present, with the exception of *I.d.* 3, which on each side is replaced by its successor. The two *I.* 1 commence to protrude behind the *I.d.* 1. In the lower jaw *I.d.* 1, *I.d.* 3, *P.d.* 3 on each side, and *P.d.* 1 on the right are replaced.

Stage II. Like I.; in addition, however, *P.d.* 1 is also replaced in the upper jaw, and the same tooth on the left in the lower. Among the adult specimens, *i. e.*, those in which the milk-dentition is replaced completely, there are several in which the skulls are shorter than that of this stage.

Stage III. Like II., with the trifling difference that *P.d.* 1 *inf.* is replaced on each side.

Stage IV. In the upper jaw *P.d.* 1, *P.d.* 3, and *I.d.* 3 on both sides, and *I.d.* 1 on the right are replaced; in the lower jaw *P.d.* 1, *P.d.* 3, *I.d.* 3, and *I.d.* 1. *I.d.* 2 is about to be shed above and below.

Microgale Cowani.

Stage I. All milk-teeth are *in situ* and functional. *M.* 2 is almost completely through the gum, and *M.* 3 is commencing to protrude.

Stage II. Milk-teeth as in I. All three molars functional. In the upper jaw *I.* 3 on the left is beginning to protrude behind and on the inside of *I.d.* 3.

Microgale Thomasi.

Stage I. All milk-teeth functional: no trace of their successors yet visible. *M.* 3 not yet completely protruded.

According to what has been stated above, in *Oryzoryctes* the milk-teeth are replaced in the following order:—*I.d.* 3, *I.d.* 1, *I.d.* 2, *P.d.* 3, *P.d.* 1, *P.d.* 2, *C.d.* In *Microgale* the replacement of *I.d.* 1 *sup.* and *I.d.* 2 takes place later, in consequence of the powerful development of its root. According to what has been stated in the case of *Oryzoryctes tetradactylus*, the milk-teeth appear in the same order as their successors.

In connexion with the foregoing a few remarks may here be introduced on tooth-formulæ and tooth-change in the Solenodontidæ and Potamogalidæ, which are closely allied to the Centetidæ.

Solenodon cubanus.—Thomas * writes the tooth-formula of *Solenodon* as follows:—

$$I.\left\{\begin{array}{ccc}1&2&3\\ \scriptstyle 1&\scriptstyle 2&\scriptstyle 3\\ \scriptstyle 1&\scriptstyle 2&\scriptstyle 3\\ 1&2&3\end{array}\right.\quad C.\left\{\begin{array}{c}1\\ \scriptstyle 1\\ \scriptstyle 1\\ 1\end{array}\right.\quad P.\left\{\begin{array}{cccc}1&0&3&4\\ &&\scriptstyle 3&\scriptstyle 4\\ &&\scriptstyle 3&\scriptstyle 4\\ 1&0&3&4\end{array}\right.\quad M.\left\{\begin{array}{ccc}1&2&3\\ &&\\ &&\\ 1&2&3\end{array}\right.$$

P.d. 3 (*auct.*) in the lower jaw is inadvertently omitted in the original.

According to this author, therefore, in both upper and lower jaws only the two posterior milk-premolars are produced. *P.* 3, Hens. (*P.* 2, *auct.*), is stated to be absent, and *P.* 4, Hens. (*P.* 1, *auct.*), to be present; this interpretation is due to the fact that the foremost *P.* is stated not to be changed. This view has been disputed by Leche †, who writes the dental formula, based upon a single specimen that he examined, as follows:—

$$I.\left\{\begin{array}{ccc}1&2&3\\ \scriptstyle 1&\scriptstyle 2&\scriptstyle 3\\ \scriptstyle 1&\scriptstyle 2&\scriptstyle 0\\ 1&2&3\end{array}\right.\quad C.\left\{\begin{array}{c}1\\ \scriptstyle 1\\ \scriptstyle 1\\ 1\end{array}\right.\quad P.\left\{\begin{array}{ccc}2&3&4\\ \scriptstyle 0&\scriptstyle 3&\scriptstyle 4\\ \scriptstyle 0&\scriptstyle 3&\scriptstyle 4\\ 2&3&4\end{array}\right.\quad M.\left\{\begin{array}{ccc}1&2&3\\ &&\\ &&\\ 1&2&3\end{array}\right.$$

It is consequently assumed that in both upper and lower jaws only the two posterior milk-premolars are present, and, moreover, that in the lower jaw the posterior *I.d.* is absent. In addition to this Leche points out as a fact especially worthy of note that all milk-teeth are of simpler structure than the corresponding teeth of the permanent set. In the young specimen of *S. cubanus* before me, the molars are indeed fully developed, but are not yet completely protruded from the jaw; the main cusp of *M.* 3 *sup.* is beginning to come through the gum. The lower molars are somewhat further advanced. Of the incisors three *I.d.* are present above and below; the lower *I.d.* 3 is situated on the outside and in front of the considerably larger *I.* 3 (which is in the act of coming through) and is about to be shed. The *C.d.* are present above and below. Of milk-premolars the two posterior are present in both upper and lower jaws; the *P.* 3, Hens., are showing. According to these facts I do not consider that we are justified in denying that the latter have precursors; on the contrary, it is probable that in the two young specimens at present known *P.d.* 3 has already been shed, like *I.d.* 3 in Leche's example. As we have seen, in the Centetidæ *P.d.* 3 is always the first among the milk-premolars to be shed; since tooth-change sets in earlier in *Solenodon*, I suspect that

* Proc. Zool. Soc. Lond. 1892, pp. 504–505.

† Anat. Anzeiger, xiii. 1897, p. 523.

in specimens with dentition less far advanced than those at present known, *P.d.* 3 will probably still be found. It therefore seems to me to be permissible to write the dental formula of *Solenodon* as follows :—

$$I.\left\{\begin{array}{ccc}1&2&3\\ \scriptstyle 1&\scriptstyle 2&\scriptstyle 3\\ \scriptstyle 1&\scriptstyle 2&\scriptstyle 3\\ 1&2&3\end{array}\right. \quad C.\left\{\begin{array}{c}1\\ \scriptstyle 1\\ \scriptstyle 1\\ 1\end{array}\right. \quad P.\left\{\begin{array}{ccc}2&3&4\\ \scriptstyle 2&\scriptstyle 3&\scriptstyle 4\\ \scriptstyle 2&\scriptstyle 3&\scriptstyle 4\\ 2&3&4\end{array}\right. \quad M.\left\{\begin{array}{ccc}1&2&3\\ &&\\ &&\\ 1&2&3\end{array}\right.$$

According to this the dentition would agree with that of *Oryzoryctes*, *Microgale*, and *Limnogale*. In comparison with those of the Centetidæ the milk-teeth of *Solenodon* convey the impression of having undergone degeneration.

Potamogale.—Nothing as yet has been published on tooth-change in this rare animal. Nevertheless I confidently assume that the teeth figured and described by Allman * and by Dobson † as permanent ones belong to the milk-dentition. Allman's specimen was not adult, and its *M.* 3 was still hidden in the jaw, as shown by Mivart ‡ and subsequently also confirmed by Allman himself §. It may here be remarked parenthetically that, in consequence of this, Jentink's *Potamogale Allmani* ‖ falls to the ground. Similarly, the dentition figured by Dobson is that of an immature specimen; according to the statement of the author referred to, *M.* 3 has not yet protruded in this example. The solitary specimen before me (Brit. Mus. no. 75, 10. 15. 4) is even somewhat younger than the examples alluded to above, since not even *M.* 2 is completely protruded; it is therefore yet younger than my specimen of *Solenodon*, in which the majority of the milk-teeth are still present. The molariform tooth standing in front of *M.* 1 is more worn than the latter, and the teeth in front of it are also worn—a further proof that we are dealing with milk-teeth.

B.

The Form of the Teeth.

The following investigation culminates in an attempt to furnish an answer to the question, whether in the Centetidæ

* Trans. Zool. Soc. London, 1866, pp 1-16, figs. 7 and 8 (pp. 10, 11).
† 'Monograph of the Insectivora,' 1882, p. 99, pl. viii. fig. 5.
‡ Journ. Anat. Physiol. ii. 1868, p. 128.
§ Proc. Zool. Soc. London, 1867, p. 256.
‖ 'Notes from the Leyden Museum,' vol. xvi. 1895, p. 234.

the tritubercular form of molar is to be regarded as primitive, or rather as the result of a process of retrogression.

I. *The Molars.*

The homologies of the cusps of the molars in the Insectivora have already been carefully studied by Mivart nearly thirty years ago *. It was shown by this author that the upper molars of *Potamogale* to a certain extent represent a transitional stage between the more complicated molars, *e. g.* of the mole, with two triangular prisms each, and the simpler ones, such as those of *Centetes* and *Ericulus*, with but a single prism:—"For each of these teeth [in *Potamogale*] have three or four very small cusps developed from the external cingulum, a very large cusp arising from the internal cingulum, and two median cusps, from each of which two slightly-marked diverging ridges proceed outwards to the external cingulum, forming two very narrow triangular prisms, so close together that a little more approximation would reduce them to a single prism, such as exists in *Centetes* and *Solenodon*." He also says:—"*Potamogale* shows . . . . . a very interesting approximation of the triangular prisms, the two external principal cusps still, however, remaining distinct, though in close juxtaposition. In *Centetes* it appears as if the concentration had been carried further, the two prisms uniting into one, as also the two external principal cusps. The single representative of these, however, has two small prominences on its inner side. In *Chrysochloris* we have the maximum of concentration, there being but a single triangular prism, the internal angle of which represents the two external principal cusps of *Erinaceus* and others, while internal to this there is but a single prominence to represent the two internal principal cusps."

I therefore have to state that Mivart long before myself, at least so far as the Insectivora are concerned, represented the complicated character of the molars as the primitive condition, and maintained that the simple form had arisen through concentration or fusion.

In opposition to this it was asserted by Huxley † that the form of molar seen in *Centetes* is the primitive one, and, as is well known, this view was subsequently supported also by Cope, Osborn, and Schlosser. Huxley terms the form in question "least-modified," and, according to him, the form of molar exhibited by all Carnivora is easily to be derived

* Journ. Anat. and Physiol. ii. 1868, p. 117 *et seq.*
† Proc. Zool. Soc. London, 1880, pp. 283–284.

from it. To his question, "Why may not *Hyænodon* and *Pterodon* be an extreme development of that type of the Insectivora which is at present represented by *Centetes*?" Winge* returned the categorical answer, "Because *Hyænodon* and *Pterodon* have not in the slightest degree a special resemblance to Insectivora, least of all to *Centetes*; there is not one single point in which *Centetes* does not stand in sharp contrast to *Hyænodon* and the Carnivora." Winge then proceeds to develop this view by interpreting the upper molars of *Centetes* in the following manner:—"The hindmost of the three outermost cusps has disappeared," he writes, "as also the posterior of the two that immediately follow these on the inner side; on the other hand, the anterior two of the original three outer cusps and the anterior of the two that immediately follow these are still present in a particularly well-developed form; we also observe remnants of a single talon, which in other Centetidæ is well developed." Consequently in the interpretation of the homologies Winge agrees in the main with Mivart.

I have shown in an accurately-drawn figure of an upper *M.* 1 of *Centetes* † that in a perfect condition this tooth, like that of *Potamogale*, possesses not less than five outer cusps; it is true that two of these are more strongly developed than the rest. In the figure in question I distinguished the main cusp of the tooth, situated on the inner side of those just referred to, by the numbers 4 + 6, in order to indicate thereby that in *Centetes* there seems to have taken place a fusion of the inner talon—6 in Winge's figures and diagrams—with the main cusp, Winge's 4.

Cope has recently ‡ reasserted his former theory, that in the existing fauna the "tritubercular" form of molar as exhibited by Centetidæ, Soricidæ, a few Lemurs, and the majority of the Carnivora is the primitive one. In Centetidæ and Chrysochloridæ the rudimentary "low cingulum" on the posterior base of lower molars and a "posterior cingulum" on upper molars are regarded as the first step towards the complication of the tritubercular molars.

M. F. Woodward § follows Mivart and Winge, since he considers the supposed "paracone" and "metacone" of *Centetes* and *Chrysochloris* to be homologous with the "ex-

* Vidensk. Meddel. fra d. naturh. Foren. i Kjöbenhavn, 1882, p. 58.

† "On *Megaladapis madagascariensis* &c.," Phil. Trans. R. Soc. Lond. vol. 185, 1894, B, p. 23, fig. 4.

‡ 'The Primary Factors of Organic Evolution' (Chicago, 1896), pp. 145, 335.

§ Proc. Zool. Soc. London, 1896, pp. 588, 589, and pl. xxvi.

ternal cingulum cusps" of *Talpa* &c., and the inner talon of *Chrysochloris*—he is not acquainted with the Centetid genera in which this is likewise distinctly preserved—with the "protocone" of *Talpa*. He regards the main cusp of the tooth of *Centetes* as homologous with the "paracone" of *Talpa*, wherein he agrees with Winge. He, however, proceeds to say:—"I do not think that the ontogeny of the trituberculate insectivore molar justifies Mivart's fusion theory, but rather suggests that this tooth corresponds only with the paracone triangle of the Mole's tooth." In other words, Woodward on the whole favours the tritubercular theory; this merely because the "paracone"—5 in his figures on pl. xxvi.—being ontogenetically the first molar-cusp to appear, he infers from this circumstance that it is the primitive cusp in a phylogenetic sense as well. He asserts, but does not demonstrate, "that as regards the primary cone, its ontogeny recapitulates its phylogeny."

That it is not merely the *anterior* "trigon" of more complicated teeth (*Talpa* &c.) with which the upper molar of the Centetidæ and Chrysochloridæ is homologous, is at once evident from the fact that the sides of the unique trigon in the latter families embrace not only the anterior but also the posterior half of the outer "cingulum-cusps."

The above-mentioned text-figure in the paper on *Megaladapis* was given by me in conjunction with four others, as representatives of four families of Malagasy mammals (belonging to three different Orders) with so-called tritubercular molars. My object was to show (1) that, as a rule, on close examination the tritubercular teeth are nevertheless found to consist of more components than only three cusps; (2) that the fact that "trituberculy" occurs in different orders is in itself sufficient to point to convergence, and the more so since the genera in question are highly specialized in other respects also; (3) that the three main cusps of the teeth with which we are dealing have *different homologies* in each of the three orders (Lemuroidea, Carnivora, Insectivora) — a further support for the assumption that convergence has taken place. This circumstance has escaped Woodward's attention, or he would hardly consider that his interpretation of the molars of *Centetes* and *Chrysochloris* brings them into complete agreement with the molars of mammals in general.

So much for the more historical part of our subject.

That the complicated mammalian molars will ultimately be traceable to a simple form I have never denied, and have even expressly stated as much; but how far back we shall have to go to find this simple condition the future will show.

For my part I have not ventured to trace the form of molar seen in Tertiary mammals to that of the older Mesozoic fossils, because, on the one hand, the hiatus between the faunæ of the Lower Eocene and those of the Jura has hitherto been too great, and because, on the other, all sorts of data are still requisite before the mammalian nature of the majority of fossil remains from the Purbeck, Stonesfield, &c. is demonstrated beyond the possibility of doubt.

We are upon firmer ground with regard to a portion of the Laramie mammals, which unhappily are for the moment still very few in number and generally isolated. Here, in the Upper Cretaceous, we meet, almost without exception, with polybunous teeth, and this, indeed, equally among the Multituberculata as among the so-called Trituberculata *; in the following comparison with the Insectivora we have to deal with the latter alone. The best-preserved upper-jaw teeth among these † are remarkable, in the first place owing to the extraordinary development of the external series of cusps, to only two of which Osborn gives names—*parastyle* and *metastyle*—while, as in the case of Didelphyidæ, Dasyuridæ, and Insectivora, from four to five cusps are present; in the second place owing to the considerable vertical and horizontal extent of the internal talon (" protocone "), which is even bulkier than in Didelphyidæ, and to which, flanking the talon on the outer side, are, moreover, superadded two smaller intermediate tubercles—the *protoconule* and *metaconule.* In correspondence with this, the talon (" talonid ") on the lower molars also is remarkably strongly developed.

Among Insectivora we meet with a similar profusion of tooth-cusps in *Galeopithecus*, *Urotrichus*, *Myogale*, &c.; these genera, however, in addition to this show specialization in the shape of a commencing solenodonty. The external cusps have diminished in bulk; similarly the talon also of the upper molars is of more moderate dimensions than in the teeth from the Cretaceous, and the " intermediate tubercles " are correspondingly enlarged. In *Myogale* the hindmost of the latter —the " metaconule "—has shifted its position more towards the inside, and, at least in the case of *M.* 1, it is almost equal to the talon in bulk: the question suggests itself whether we may not find herein an indication of the mode of origin of many " quadritubercular " mammalian molars.

Potamogale.—In this genus, as has been mentioned above,

* H. F. Osborn, " Fossil Mammals of the Upper Cretaceous Beds," Bull. Amer. Mus. of Nat. Hist. vol. v. 1893, pl. viii.

† *Loc. cit.* pl. viii.

the tubercles of the second series from without—the "paracone" and "metacone"—are found to be in close juxtaposition; the talon has diminished in size, but nevertheless attains to about two thirds of the height of the "paracone." Intermediate tubercles as such are not present; on the other hand, from both sides of the talon, in the neighbourhood of which they broaden out to a certain extent, two basal ridges run towards the exterior along the anterior and posterior margin of the tooth, the anterior one reaching the external margin, while the posterior ends at about the middle of the tooth.

Solenodon.—The "paracone" and "metacone" are fused together, in consequence of which the molars have become still narrower than in the foregoing genus. The talon, too, has diminished still further in height and extent. The posterior basal margin ends on the inside, in line with the talon, in a more feebly developed tubercle, the homologue of the "metaconule" of *Myogale.*

In *Centetidæ* the "paracone" and "metacone" likewise appear to be fused together. That it actually is a case of fusion, *i. e.* that the main cusp of the molars is not to be regarded as homologous with the "paracone" alone, is shown, on the one hand, by the state of things in *Potamogale*, in which the molars in this and other respects occupy an intermediate position between those of Insectivora with "paracone" and "metacone" widely separated one from another and those with an unpaired main cusp (Solenodontidæ, Chrysochloridæ, Centetidæ), and, on the other, by the condition seen in *Oryzoryctes.* In the intact *M.* 1 of this genus, as also in the intact *P.d.* 1—in the case of *O. hova* more distinctly than in that of *O. tetradactylus* and *O. niger*—the "paracone" appears bicuspid; the posterior cusp is much less developed than the anterior, and, as in the case of *Potamogale*, is shifted somewhat further than the latter, towards the outside. In *Oryzoryctes* this metacone occurs besides in *P.d.* 2 (Hens.) and *P.d.* 3 (Hens.), and is seen with great distinctness in their successors *P.* 2 and *P.* 3. In the case of *Microgale* I find that it is present neither in the molars nor in the premolars, with the sole exception of *P.d.* 2 (Hens.).

The talon ("protocone") in Centetidæ is reduced still further than in *Solenodon,* until it entirely disappears (*Centetes*); on the other hand, in the latter genus the anterior and posterior basal ridges on both sides of the internal base of the united para- and metacone swell up in the shape of cusps, the posterior to a greater degree than the anterior; the former appears as an independent cusp on *P.* 1 and *P.* 2.

Since the united para- and metacone extends to the inner margin of the tooth, and the "protocone," from *Potamogale* onwards, appears more and more coalesced with the former, it is probable that the continually diminishing "protocone" has gradually been absorbed by the para- + metacone. The state of the case in the molars of *Ericulus* and *Echinops* is similar to that which is seen in *Centetes*; there is no occasion here to go further into details.—In *Oryzorycetes* the protocone is still of relatively considerable size, bicuspid in the case of the two anterior molars and in *P.* 1, most distinctly so in the latter; the posterior cusp, which appears unusually little developed in *M.* 1 and *M.* 2, will have to be interpreted in the same manner as in *Solenodon.*—In *Microgale Dobsoni* also the feebly developed talon is bicuspid.—In *Limnogale* it is even tricuspid in the case of perfect teeth.—The maximum of reduction seen in Centetidæ occurs in *Hemicentetes.* The talon is still indicated only in the case of *M.* 1; the external cusps, with the exception of two, on the anterior and posterior margin, are to all intents and purposes suppressed; the united para- and metacone is of considerable height. Moreover the teeth are compressed longitudinally, parallel to the longitudinal axis of the body, the last two upper molars less so than the rest.—*Geogale* is not known to me by personal examination.

After the above analysis of the molar components in the Centetidæ it is not difficult to give an answer to the question with which we started—namely, whether the form of molar that occurs in this family (as also in the Solenodontidæ and Chrysochloridæ) is to be regarded as primitive, as is pretty generally assumed, or, rather, as the result of a reduction. It is manifest that it is only the richly developed external cusps which are a primitive feature, because, indeed, throughout the mammalian class these cusps present themselves as an archaic phenomenon. I do not venture to go so far as Winge, who regards them as homologous with the three cusps of the *Triconodon*-tooth. But we found them developed to the fullest extent in Laramie teeth, next to which they are most pronounced in the low groups Polyprotodontia and Insectivora; in other orders in the case of their oldest representatives.

Undoubtedly of a secondary character, and to be regarded as a retrogression, is, according to what has already been stated, the fusion of the "paracone" and "metacone"—a phenomenon met with elsewhere among mammals only in premolars and rarely in the *M.* 3 *. The united para- and

* It is only in *Notoryctes,* which in other respects also is highly

metacone, which in Centetidæ continually advances further inwards, gradually replaces in function the "protocone" (talon), which in consequence becomes superfluous. In the interpretation of the homologies the two have been pretty generally confounded with each other, *i. e.* paracone + metacone is regarded as the "protocone."

As I would finally point out yet once again, the three main cusps of the crown—upon which the theory of the tritubercular form of the dentition of Centetidæ is based—accordingly consist externally of the two most strongly developed of the outer cusps, the *parastyle* and *metastyle* of Osborn, and internally (apex of the triangle) of the paracone + metacone, united to form a single cusp. In cases where similar forms occur among the Lemuridæ the two outer cusps are constituted by the paracone and metacone. Like Winge, I have interpreted * the apex in Lemuridæ as being homologous with the "protocone" of other mammals—Winge's 6.

With regard to the *lower molars* I can express all that I need to say here in a very few words. A characteristic feature in these teeth is the extensive reduction exhibited by the "talon," which usually appears only as a low posterior basal cusp. The lower molars, therefore, essentially consist of the anterior trigon (Osborn's "trigonid") alone. When we consider that the talon (Osborn's "talonid") is developed to the fullest extent among mammals belonging to the Lowest Tertiary † and Upper Cretaceous ‡ Beds, it appears, in connexion with all that has been stated above in the case of the upper molars, unjustifiable to wish to regard the form of the lower molars in Centetidæ as of a primitive type.

II. *The Antemolars.*

Leche remarks § with reference to the upper incisors and canines of Centetidæ (*Microgale*, *Ericulus*, *Centetes*), that they are provided with accessory cusps more abundantly in

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specialized and forms a parallel to Centetidæ, and still more to Chrysochloridæ, that this fusion likewise occurs in all molars; the protocone in *Notoryctes* is still developed to a considerably greater extent than in Centetidæ.

* "On *Megaladapis* &c." (*vide suprà*), p. 23, text-figs. 1 and 2.

† *Cf.* Lemoine, "Etude d'ensemble sur les dents des Mammifères fossiles des environs de Reims," Bull. Soc. Géol. de France, 3e série, t. xix. 1891, pls. x., xi.

‡ *Cf.* H. F. Osborn, "Fossil Mammals of the Upper Cretaceous Beds," Am. Mus. Nat. Hist. vol. v. art. xvii. (New York, 1893), pl. viii. figs. Hl, Al.

§ Anat. Anz. xiii. p. 520.

the milk-dentition than in the permanent set. This applies on the whole to the same teeth in the lower jaw also, as well as to the milk-premolars. Moreover, before proceeding to discuss the facts of the case somewhat more in detail, I would premise, by way of a general observation, that in the Centetidæ there is rather less difference between the accessory and the main cusps (the former being more, the latter less strongly developed) in the milk- than in the permanent dentition.

1. *Upper Jaw.*—The least divergence in form between the premolars and molars is found in *Echinops*, the premolars of which differ to an extraordinary degree from those of *Oryzoryctes hova*, which in this respect forms the opposite extreme. The closest approach to *Echinops* is exhibited by *Ericulus*.

In *Echinops* and *Ericulus, P.* 1 (Hens.) is hardly distinguishable from *M.* 1; the difference from the molars—and from *P.d.* 1—to be discussed later on, in the position and height of the antero-external cusp, is demonstrable only in teeth which are intact. In both genera *P.* 1 is somewhat longer than *M.* 1, and in *Echinops* it is also somewhat broader (in the transverse direction) than the premolar of *Ericulus*; in the former there is found a low "protocone" and "hypocone."

In *Ericulus P.* 2 already assumes the form of a carnassial; this is much less the case in *Echinops*, in which the same tooth is as yet more like a molar, since here the antero-external cusp does not extend so far forwards, and the whole tooth appears altogether less elongate than *P.* 2 and *P.d.* 2 of *Ericulus* (I am not acquainted with *P.d.* 2 of *Echinops*). *P.* 2 of *Echinops* has in addition a distinct internal cusp ("protocone"), and that of *Ericulus* has two such cusps like *P.* 1 of *Echinops*.

P. 3 of *Echinops* resembles a carnassial; but the antero-external cusp is very slightly marked. Three roots are present, and the inner one bears a fairly large internal cusp. The milk-tooth agrees with its successor in form.

In comparison with *P.* 3 of *Echinops*, the corresponding tooth in *Ericulus* is somewhat reduced, and the secodont form begins to be seen: the longitudinal diameter is the greater, while in *Echinops* the transverse expansion is the more pronounced. There are but two roots. A feebly developed basal margin, as the remains of an internal cusp, is confined to the posterior half of the inner side. A remnant of the external cusps, likewise limited to the posterior half of the tooth, is present, as well as in many cases a feeble antero-external cusp besides. The milk-tooth is similar in shape; only the external cusps and the internal cusp are more strongly developed; it is also provided with an anterior basal cusp.

The remains of the external cusps are even yet occasionally found in the case of the *C.d.* of both genera; for *Ericulus* see Leche's paper *; they are still better developed on the *C.d.* of *Echinops,* which likewise possesses in addition a slight anterior basal cusp. On the *C.d.* of both genera are also found remains of an interior basal cusp.

Centetes.—As in the case of *Echinops* and *Ericulus*, *P.* 1 *sup.* differs very little from the milk-tooth and from *M.* 1; it is true that here also the antero-external cusp is somewhat more independent and is placed higher up, but the difference is perceptible only in teeth which are intact. Apart from this, the tooth is more quadrate in outline, and the triangle formed by the external cusps and the united para- + metacone does not project so far towards the interior as in its precursor in the milk-dentition and in the molars.—*P.* 2 is the largest and tallest in the molar series; it possesses a fairly large postero-internal cusp, as well as a minute anterior basal cusp; of the remaining external cusps only a single one, confined to the postero-external angle, is present. The transition in form between this tooth and the small secodont *P.* 3, in which the anterior basal cusp is wanting or only just indicated, is quite abrupt. It is different in the milk-dentition: *P.d.* 2 is a tooth of a very elongated shape, with external cusps better developed than in the case of its permanent tooth; the foremost of these particularly is more strongly developed than in the latter, and especially than in the permanent tooth of *Ericulus* and *Echinops.*—*P.d.* 3, although already strongly compressed longitudinally, and without, or only with a slight indication of an anterior basal cusp, still shows in fresh specimens traces of the postero-external cusps; it exhibits, further, a remnant of an internal cusp, and, lastly, an accessory cusp behind and below the main cusp (as on *P.d.* 2, *P.d.* 3, *P.* 2, and *P.* 3 of *Oryzorycetes*—see below); this, however, is wanting on certain specimens, in which case the posterior basal cusp is more strongly developed.—Of the milk-incisors the foremost pair alone possesses a distinct posterior basal cusp; in the case of *I.d.* 2 and *I.d.* 3, which in the fresh condition are uncinate and recurved, this is scarcely indicated. On the other hand,

* Anat. Anz. xiii. p. 521, fig. 4.

contrary to what is stated by Leche *, younger specimens of *I.* 1 and *I.* 2 always possess a well-developed posterior basal cusp.

In the case of *Oryzorycles*, *Microgale*, and *Limnogale* *P.* 1 may at once be distinguished from *P.d.* 1 by the fact that it resembles *M.* 1 much less than the latter does, which is especially evident in the condition of the external cusps; the foremost of these lies, in the case of *P.d.* 1 and the two anterior molars, in the same longitudinal row as those following it; in the premolar it is set higher up and is separated by a greater gap from those behind. As already mentioned, this difference is much less distinct in the case of *Centetes*, *Ericulus*, and *Echinops*.

The number of the external cusps on fresh cheek-teeth of the molar series is from four to five in *Microgale*, on *P.d.* 1 usually five; in *Oryzorycles* five on *P.d.* 1, as on *M.* 1 and *M.* 2. These external cusps are divided by a median gap into an anterior and a posterior series; where five cusps are present, there are in some cases two cusps in the anterior and three in the posterior division—in others the reverse. In *P.* 1 only three external cusps are found; in the case of *Microgale* the median one, in comparison with that on either side of it, has become disproportionately large and lofty. With reference to the various species of *Microgale* the following remarks must be made. *M. Dobsoni*: *P.*1 corresponds in its carnassial-like condition pretty closely with the *P.* 2 of *Ericulus*, and similarly *P.* 2 of *M. Dobsoni* is almost identical with the *P.* 3 of *Ericulus*; at the most, in the case of the former, the internal cusp is somewhat more strongly developed; nevertheless in the latter also the tooth, as already mentioned, has but two roots. *P.* 3 is a secodont tooth with two roots; this applies to all species of *Microgale*.—In *M. Cowani* *P.* 2 differs but little from *P.* 1; in height especially the two teeth are about equal, while in *M Dobsoni* *P.* 2 is much lower than *P.* 1. *P.* 2 is only slightly more compressed, and in consequence somewhat more elongate; the "protocone" is developed to precisely the same extent as on *P.* 1. A much greater amount of compression is shown by *P.* 2 in the case of *M. Thomasi*, in which also the "protocone" is unusually reduced in comparison with that of *P.* 1. In the genus *Microgale* the maximum of compression (parallel to the longitudinal axis) is found in the case of *M. gracilis*; nevertheless a feebly developed "protocone" is still present on *P.* 2, while in the case of the tooth

* *Loc. cit.* p. 519.

of *M. pusilla*, which in other respects has undergone less compression, this has disappeared.

In the case of *Oryzoryctes tetradactylus* and *O. niger* the compression of *P.* 1 has proceeded still further, as is shown *inter alia* by the considerable reduction of the median external cusps; as in *Microgale*, three of these cusps are present on *P.* 1 of *Oryzoryctes*, but the middle one is not so predominantly developed as in the case of the former genus; the first is somewhat larger, the second smaller than in *Microgale*. The "protocone" still has the same extent as on *M.* 1 and is bicuspid. Owing to its more compressed form *P.* 1 agrees much more closely with *P.* 2 of *Microgale* than with *P.* 1 in the latter genus. *P.* 2 has undergone even more compression: the median external cusps are distinguishable merely as vestiges on teeth which are intact; the "protocone" is reduced to a minimum. The perfectly secodont *P.* 3 is of considerable height; it projects above *P.* 2. Both *P.* 2 and *P.* 3, as well as their precursors, show on the blade, behind the main cusp and halfway up between this and the alveolar margin, an accessory cusp, the interpretation of which as the homologue of the metacone of the molars has already been discussed.—In *Oryzoryctes hova* even *M.* 1 already exhibits the general outlines of a carnassial tooth. In *P.* 1 the compression in the longitudinal direction has made to a certain extent still further progress than in the case of the other species; the "protocone" is likewise bicuspid. *P.* 2 is altogether secodont, without a trace of median external cusps or "protocone."

2. *Lower Jaw.*—In *Echinops* and *Ericulus P.* 1 and *P.* 2, as well as their precursors in the milk-dentition, resemble molars; accordingly even *P.* 2 is provided with a stout internal cusp, Osborn's metaconid, of which a trace is still present even on *P.* 3 of *Echinops*. In the case of *Ericulus P.d.* 3, *P.* 3, *C.d.*, and *C.* have an internal basal margin, which is still present on the incisors also; it is much less pronounced in *Echinops*. *P.* 3 of *Echinops* has sometimes only one root. The canine, which is always single-rooted, exhibits now and then a slight median groove down the root.

Centetes.—Both *P.* 1 and *P.d.* 1 are molariform, but *P.* 1 is larger than the molars. *P.* 2 is a powerful tooth, almost resembling a canine; like the corresponding tooth in the upper jaw, it is higher than the posterior molars. An indication of an anterior basal cusp is found only in certain cases; a posterior basal cusp is present in the form of a talon, which occupies the entire breadth of the tooth. Lastly, a slight internal tubercle ("metaconid") also occurs. *P.* 2 differs from *P.d.* 2 to a not inconsiderable extent; the latter is elongated, with a strongly developed anterior basal cusp, and possesses an accessory cusp situated on the same level as the "metaconid" (but on the outer side of the main cusp), than which it is sometimes rather more, sometimes rather less strongly developed. The dimensions of *P.* 3 are variable, but this tooth is always smaller than *P.* 2; an anterior basal cusp is indicated now and then, and sometimes an accessory cusp in addition, behind and below the main cusp. The latter is on *P.d.* 3 sometimes of really considerable bulk, and almost as strongly developed as on *P.d.* 2; on other specimens no trace of it is to be seen. Occasionally, even on perfectly fresh teeth, there is no vestige whatever of an anterior basal cusp in the case of *P.d.* 3 (*cf.* Leche, *loc. cit.* p. 519).

These variations, as well as the similar ones in teeth belonging to the upper jaw, suggest the idea that we have to deal with more than one species. I may add that I assume the existence of two species of *Centetes* for reasons other than those advanced by Bardeleben, but I cannot here enter further into this question.—All three milk-incisors show, as do their successors, a posterior basal cusp.

Microgale.—*P.* 1 alone is molariform, and consequently provided with an internal cusp ("metaconid"), which is wanting in the case of the two anterior premolars, but, in the majority of species at any rate, is still present on *P.d.* 2. *P.* 2 is somewhat larger than *P.* 3, but in other respects the two teeth are alike: they are secodont, with a median main cusp, an anterior and posterior basal cusp, and two roots. It is only in the case of *M. pusilla* that *P.* 3 has a single root and is similar in build to the *C.*, *i. e.* not elongate, but shortened and inclined obliquely forwards; the anterior cusp is indicated only by a slight indentation in the margin, which occurs high up near the main cusp. As regards the form of *P.* 3, *M. longicaudata* forms a transition between *M. pusilla* and the remaining species (*M. Dobsoni*, *Thomasi*, *Cowani*, *gracilis*, and *longirostris*).

Oryzoryctes.—In the build of the lower premolars this genus agrees essentially with *Microgale.* In comparison with *P.* 2, *P.* 3 is somewhat simplified, owing to the fact that the basal cusp is absent or scarcely indicated. A characteristic feature in the dentition of *Oryzoryctes* is the unusually large and powerful *C.* in both upper and lower jaws; in the case of

O. hova this tooth is even somewhat more strongly developed than in that of the other two species. (The *C.* of *Microgale* is generally much feebler—fairly stout only in *M. pusilla.*) The tip of the *C.* of *Oryzorycles* is recurved, more so in the lower than in the upper one. All the canines have a posterior basal cusp, which is more strongly developed in those of the upper jaw.—The upper *I.* 1 converge towards each other and are provided with a strongly developed posterior basal cusp; *I.* 2 has, as in the case of *Microgale* (*cf.* Leche, *loc. cit.*), an anterior and a posterior basal cusp, of which the former is still present even in the feebly developed *I.* 2 of *M. gracilis*. *I.* 3 is rudimentary, with indications of anterior and posterior basal cusps. Of the lower *I.* the middle one is the strongest, the hindmost the weakest and similar in form to *I.* 3 *sup.* *I.* 1 and *I.* 2 are provided with a posterior basal cusp (*I.d.* 2 appears to possess two).

Thus we see—to recapitulate the morphological relations of the premolars, at least for the extremes of our series—that *P.* 1, *P.* 2, and *P.* 3 in the upper jaw (*M.* 1, *P.* 1, and *P.* 2 in the lower) of *Echinops* correspond to *M.* 2, *M.* 1, and *P.* 1 of *Oryzorycles hova* in general form, and therefore without doubt in function also. Analogues of the two secodont teeth —*P.* 2 and *P.* 3 *sup.*—of *O. hova* are entirely wanting in *Echinops*. As has been mentioned above, the *C.d.* of *Echinops* and *Ericulus* are still more premolariform than those of all other Centetidæ which have here been discussed, while their *I.*, in the permanent set at least, are not more complicated than those of *Microgale* and *Oryzorycles*—rather the contrary. Up to a certain point, therefore, in the case of *Echinops* and *Ericulus*, *C.* and the posterior *I.* assume the functions exercised by the anterior premolars in the case of other genera.

This condition *partly* coincides with that to which Leche has drawn attention and termed "release (*Entlastung*) and reduction of the middle antemolars with simultaneous higher development of the anterior incisors" *, which we now have briefly to discuss.

According to Leche's detailed account of this process †, the part played therein by the lower *I.* 1 and *C.* is especially characteristic. "The former," he writes, "is reduced to the same extent as *I.* 2 is developed, and it finally disappears altogether, so that in the lower jaw it is *I.* 2 that attains to the degree of development corresponding to that of the upper

* Anat. Anzeiger, xiii. 1897, pp. 521, 522.

† "Zur Entwicklungsgeschichte des Zahnsystems der Säugethiere &c.: I. Ontogenie," Bibl. Zool. Heft 17, 1895, p. 39.

I. 1. In connexion with this process *C.* exhibits all gradations from the typical development down to complete agreement with the surrounding incisors or premolars." In his subsequent paper the author in question states that *Echinops* is the only member of the Centetidæ that has taken this direction.

A somewhat similar state of things is found among Centetidæ also in the case of *Microgale Dobsoni* and *Limnogale.* Besides, in the various genera that here come under consideration we are confronted with slightly different processes, which must be kept distinct. A commencement in the direction of *Echinops* is already perceptible in the case of *Ericulus*, since the upper *I.* 1 and the lower *I.* 2 have increased in strength, although they do not, as in *Echinops*, surpass the corresponding *C.* In both genera *I.* 1 *inf.* has been but little affected, though the upper and lower *I.* 3 (and *I.d.* 3 previously) have suffered all the more and have been completely suppressed. The case is much the same with regard to *M. Dobsoni.* It is true that here we still have three incisors above and below, but the lower *I.* 3 is a very inconspicuous tooth, which in old individuals may be wanting on one or both sides. The upper *I.* 1 and the lower *I.* 2 are very powerful; the former is longer than *C.*, as in *Echinops*, but *I.* 2 *inf.* also overtops considerably the lower *C.*, while in *Echinops* both teeth are of equal strength, and in *Ericulus C.* is the larger.—In *Limnogale* the conditions are somewhat different. Here also the lower *I.* 2, like the upper *I.* 1, have been more powerfully developed than *C.*; but in the upper jaw the two posterior *I.*, the canine, and the anterior premolar have all become practically equivalent in size and form, have assumed almost the shape of canines, with recurved tips. The corresponding milk-teeth of *Limnogale* differ to no very great extent from the permanent ones, but are somewhat more dissimilar in themselves. The same statement applies to the lower *I.* 3, *C.*, and *P.* 3. The latter, which otherwise throughout the Centetidæ, with the exception of *M. pusilla* and now and then of *Echinops*, has two roots, in *Limnogale* (I have only one adult specimen before me) has a single root. Its precursor in the milk-dentition possesses in one instance two closely approximated roots; in a second example it, like *P.* 3, is single-rooted. Even the middle lower premolar (*P.* 2, Hens.) of *Limnogale* shows an approach to the form of the antemolars in front of it, and, like its precursor *P.d.* 2, it is without the internal cusp (" metaconid ").

The analogy between *Limnogale* and *Potamogale* in the condition of the antemolars is obvious. In both genera we find in the upper jaw, behind the large canine-like *I.* 1, and in the lower jaw, behind the similarly constituted *I.* 2, a series of four teeth, which, especially in the upper jaw, are very similar to each other, as an adaptation to the conditions under which these two amphibious Insectivores obtain their food, and to the change in their diet. We are confronted with a degeneration, but in combination also with adaptation, whereby (especially in the case of *Potamogale*, which appears to be more exclusively piscivorous than *Limnogale*) an approximation is furnished to the dentition of the Pinnipedia *. There is, however, this difference, that while in the case of the latter the *entire* dentition is now exclusively subservient to the functions of seizing and holding, in the Insectivores in question these are confined to the antemolars, since, as proved by the number and shape of their molars, they cannot, for the present at any rate, dispense with the *masticatory* apparatus.

LXVI.—*Descriptions of new Bats and Rodents from America.* By Oldfield Thomas.

Dasypterus ega xanthinus, subsp. n.

Apparently similar in all essential characters to *D. e. typicus*, in spite of the wide difference in locality, but distinguished by the clearer yellow of the back, gradually brightening backwards until on the hairy part of the interfemoral the fur is quite fulvous. Under surface dull fulvous from chin to anus, the belly-hairs blackish basally, then light fulvous gradually deepening to their tips. In the typical South-American forms the back is dirty whitish, with dark tips to the hairs, and there is little or no fulvous on the under surface.

Dimensions of the type (male):—

Forearm 47 millim.

Head and body † 68; tail † 48; hind foot with claws † 10; ear † 16.

Skull: greatest length 16·2, greatest breadth 11·4; breadth of rostrum at posterior edge of large premolar 7.

Hab. Sierra Laguna, Lower California. Six specimens examined.

D. ega is not included at all in Mr. G. S. Miller's admirable monograph of the Vespertilionidæ found north of Panama, so that its occurrence in Lower California is a most remarkable and unexpected fact, considering the extent and completeness of the collections he worked from.

* As regards the Pinnipedia *cf.* W. Leche, 'Zur Entwicklungsgeschichte des Zahnsystems der Säugethiere, I.' (Stuttgart, 1895), p. 66.

† Measured in flesh by collector.